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1160 W. Orange Grove Ave., Arcadia, California, U.S.A. 91006

THE ORIGIN OF AUTUMNAL "FALSE BROODS" IN COMMON PIERID BUTTERFLIES

ARTHUR M. SHAPIRO

Department of Entomology and Limnology, Cornell University, Ithaca, N.Y. 14850

"False broods" of common Pierid butterflies have received frequent comment in the literature (Clark 1932, Clark & Clark 1951, Rawson 1945, Shapiro 1962, 65, 66). Shapiro (1962) speculated that November and December emergence of *Colias eurytheme* Boisduval at Philadelphia, Pennsylvania resulted from premature development of pupae which would have overwintered under normal circumstances. It was suggested that such pupae had developed nearly to the point of eclosion before being arrested by the onset of cold weather. A subsequent mild spell of sufficient duration would allow them to resume their development and eclose as a late autumn "false brood." Circumstantial evidence to this effect was presented in a later note (Shapiro 1965). The present paper demonstrates that successful eclosion occurs after prolonged thermal arrest of development, and that unfed adult *Colias* are capable of prolonged survival at sustained low temperatures. Similar phenomena are reported for non-diapausing pupae of *Pieris rapae* Linnaeus and *P. protodice* Boisduval and LeConte, and their respective adults.

COLIAS EURYTHEME

"False broods" have been reported for this butterfly in a variety of localities (various authors *in litt.*). The phenomenon is probably general in "protected" microhabitats at the end of the season, throughout the northern part of the species range. Characteristics of the emergence are noted in another section, below.

Ova were obtained from four wild females (one *alba*) collected at Erdenheim, Montgomery County, Pennsylvania, 26 November 1967. The larvae were reared at Ithaca on alfalfa, *Medicago sativa* L., at 75°F. in 16 hours light on a 24-hour cycle. The first pupa was formed 20 December and the last 5 January 1968.

Forty-nine pupae were obtained. Sixteen of these were held at 75°F. until a well-defined discal orange flush appeared on the wings, but before the deposition of black border pigment had begun. They were then chilled rapidly to, and held at 36°F. An additional sixteen were allowed to develop full black borders before being chilled to the same temperature. The use of pigment development as a criterion of general condition excluded *alba* females from the first, but not the second group. The remaining seventeen pupae were used as controls. Ten were permitted to develop to eclosion at 75° while seven were chilled 72 hours after pupation, well before the appearance of any wing pigment.

In the two groups of sixteen, four pupae selected at random were removed weekly for each of four weeks and allowed to complete their development at 75°. In both groups all the pupae eclosed, and no cripples were obtained until the third week; even in the fourth only three of the eight butterflies were defective. Most of the pupae which were arrested when less advanced eclosed within 60 hours, regardless of the duration of the arrest, and all within 72 hours. The more advanced pupae all eclosed within 36 hours, mostly within 24; four were observed to eclose within one hour, and one within 35 minutes.

The seven pupae refrigerated at 72 hours were removed after three weeks of developmental arrest. Three were permitted to eclose at 75°, which they did within six days. The remaining four were re-arrested for one week after both orange and black wing pigment had developed. These all eclosed; two were slightly crippled. The ten unarrested pupae produced normal butterflies in seven to ten days.

Three of each group of four butterflies were chilled to 36° within twelve hours after eclosion, unfed and unflown. Eight of the ten 75° butterflies were similarly treated. The remaining butterflies in each group were held unfed and unflown in the dark at 75°. The insects were all examined daily. All controls died within seven days.

Greatly extended survival was noted at 36°; refrigerated butterflies lived from 24 to 49 days. The survival of the butterfiies

from previously arrested pupae is summarized in Fig. 1. The unarrested insects lived from 33 to 47 days. Length of adult survival in refrigeration was approximately inversely related to duration of pupal arrest on a day-for-day basis. All of the four-week-arrest insects died within 31 days. Crippling and survival data for these experiments are summarized in Table I.

PIERIS RAPAE AND *P. PROTODICE*

Ten pupae of each of these species, reared in diapause-inhibiting conditions (75°F., 16-hour photoperiod) were arrested at 36° for three weeks at the stage when white, but not black, pigment had been laid down in the wings. The pupae were selected at random from Cornell cultures of the two species, *P. rapae* from third-generation Ithaca, and *P. protodice* from thirteenth-generation Philadelphia stock. Fifteen normal eclosions were obtained within 80 hours. The remaining five butterflies (four *protodice,* one *rapae*) were variably crippled. One of each sex from each batch of normals was held unfed in the dark at 75°; all four died within seven days. The remaining normal insects (four *protodice,* seven *rapae*) were chilled to 36° within twelve hours after eclosion and held at that temperature. *P. protodice* survived 13-26 days and *P. rapae* 15-27.

The Role of Pupal Diapause. — Throughout the Middle Atlantic states, the three species discussed are normally the last non-hibernating butterflies on the wing in autumn. At Philadelphia the last *Pieris* (both spp.) are generally taken from two to four weeks before the last *Colias,* rarely as late as the third week of November. At Ithaca, north of the breeding range of *P. protodice, P. rapae* disappears only a few days before *C. eurytheme;* the latest record is 1 November (1967). The mean last capture date for *P. rapae* at Philadelphia in 1959-66 was 12 November, and at Ithaca in 1966-67, 29 October. *Pieris* possesses a facultative pupal diapause mechanism (Barker, Mayer, & Cohen 1963; Shapiro, in preparation) which is lacking in *C. eurytheme.* Diapause is induced by long nights (greater than approximately 11 hours), but inhibited by high temperatures. Under constant laboratory conditions, night lengths from twelve to eighteen hours are equally effective in inducing diapause below inhibition-threshold temperatures. If all of the late larvae in both localities were exposed to diapause-inducing photoperiods, the difference in mean last adult date should reflect the onset of temperatures permitting all pupae to diapause. On the

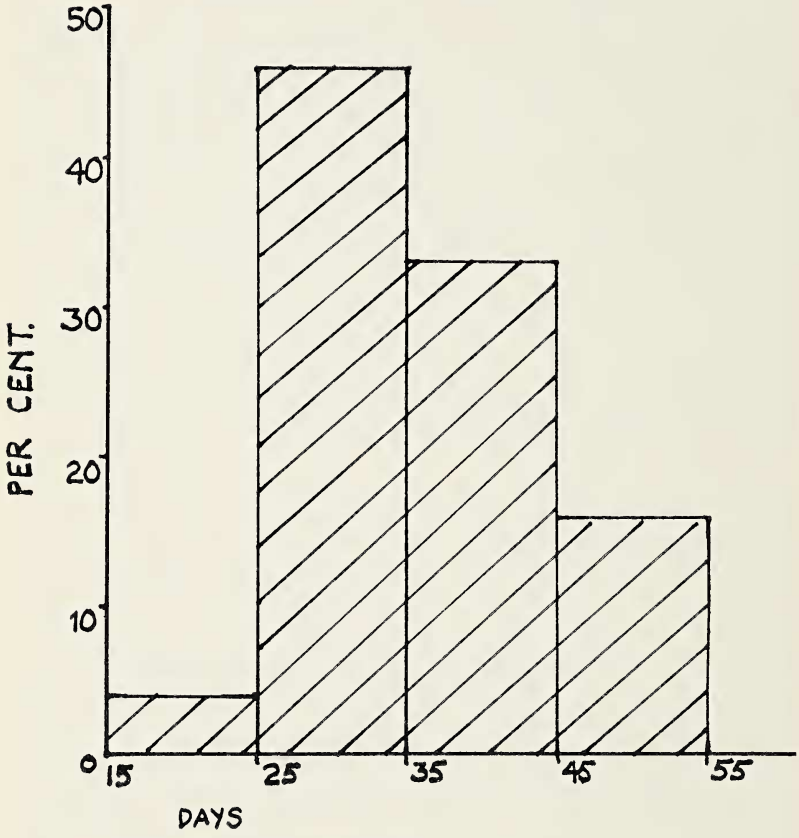

Fig. 1 Survival of 24 *Colias eurytheme* held at 36°F.

Period of Arrest (Days)	Normal	Crippled	Number of Adults Chilled	Mean Survival (Days)
Adults:				
I. Chilled with orange pigment only				
7	4	0	3	45.3
14	4	0	3	40.7
21	3	1	3	35.0
28	3	1	3	29.7
II. Chilled with orange and black pigment				
7	4	0	3	44.3
14	4	0	3	37.7
21	4	0	3	28.8
28	2	2	3	25.7
III. Control				
Unarrested	10	0	8	41.3

Table I.

Crippling and adult survival in Colias eurytheme with thermally arrested pupal development.

basis of laboratory growth rates, an estimate of three weeks prior to the mean last date, corresponding to the larval sensitive period of the last emergents, has been made for each locality. Assuming 100% threshold temperatures are the same in both stocks, these two dates should show similar temperature characteristics. The dark period for both is more than twelve and one-half hours, well above the diapause-induction threshold, and the mean temperatures (based on thirty-year United States Weather Bureau data) for Philadelphia, 21 October, and Ithaca, 8 October, differ by only one degree F. One may conclude that an effective 100% diapause is obtained above the threshold night length when the mean temperature reaches the mid-50s. The late-season emergences of *Pieris* are probably analogous to those of *Colias,* but must originate from non-diapause pupae. The phenology of *P. protodice* at Philadelphia is being studied in detail for presentation elsewhere (Shapiro, in preparation).

Temperature Correlations in Colias. — "False broods" of *C. eurytheme* occur regularly at Philadelphia under particular weather conditions in late November, and frequently as late as the first week of December; the latest on record is 16 December (1959). In Tompkins and Cortland Cos., central New York where winter survival of *C. eurytheme* is poor and the population may be replenished annually by immigrants from the south or west, the latest known record is 12 November (1967); the cutoff seems to be generally about 1 November. There is thus a 3- to 4-week difference in the average date of last flight between the two localities. As photoperiodically controlled diapause cannot be invoked, an absolute dependence on temperature would be expected to dictate the end of the season. Mean temperatures and freeze data, based on thirty-year United States Weather Bureau records, were compared for the two localities (Table II). The mean temperature for the last ten days of November at Philadelphia is 40.7°F.; for the last five days of October and the first five of November at Ithaca, 44.8°F. The mean reaches 40° at Ithaca on 12 November. *C. eurytheme* thus disappears in warmer conditions at Ithaca than at Philadelphia, based upon means. The thirty-year mean date of first frost (32°F.) at Ithaca is 4 October and at Philadelphia 25 October. The cutoff for autumnal *Colias* therefore occurs about four weeks after the mean first frost at each locality, the frost dates being three weeks apart. There is no good correlation with the onset of lower sub-freezing temperatures. The deviations below 32° for low temperatures on all sub-freezing nights prior to the 1967

Station	Freeze Threshold Temperature F°	Mean date of first autumn occurrence	Mean number of days between last spring and first fall occurrence
Philadelphia, Pa. (Shawmont)	32	10/25	192
	28	11/09	223
	24	11/23	250
	20	12/06	272
	16	12/17	287
Ithaca, N. Y. (Caldwell Field)	32	10/04	145
	28	10/21	181
	24	11/05	207
	20	11/21	237
	16	11/29	255

Table II.

Freeze data for two stations, 1929-1959. From U. S. Dept. of Commerce, Weather Bureau, Climates of the States, Pennsylvania and New York, 1960.

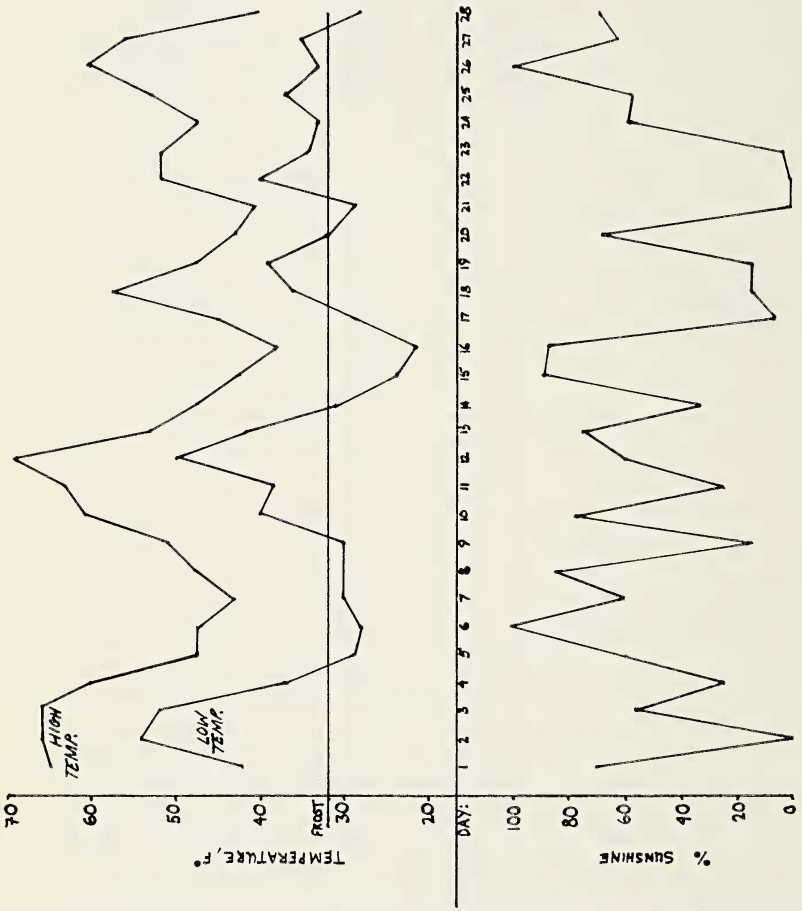

Fig. 2. Weather conditions, November 1-28, 1967. U. S. Weather Bureau, Philadelphia, Pa.

cutoffs summed to 41° at Philadelphia and 44° at Ithaca. If this close agreement is general it would imply that the sequence of temperatures acts in a cumulative way to end the season, perhaps by selective mortality of the most advanced pupae. Degree-hours below freezing might be expected to be a still more sensitive indicator. Close study of day-to-day temperature patterns, including the correlation of data for successive days, should reveal more about the critical factors.

It is easily demonstrable that single frosts, even a severe freeze, do not prevent the subsequent eclosion of autumnal *C. eurytheme*. Fig. 2 shows the weather at Philadelphia during November 1967. Eleven frosts occurred prior to the emergence on the 26th, the most severe reaching 22°F. on the 16th. Fig. 3 shows temperature data for parts of October and November, 1967 with two-hour *Colias* collection totals for each day in the field in upstate New York. At Ithaca there were nine frosts between 12 October and 12 November, with the lowest temperature 23° on 30 October and 7 November.

Case Histories. — The 26 November 1967 emergence was a typical "false brood" at Philadelphia. Butterflies were taken at Erdenheim and Cheltenham, Montgomery County, at localities which regularly produce the earliest vernal and latest autumnal *Colias* I have taken on the southeastern Pennsylvania Piedmont. Both consist of rolling, grassy meadows open to the south and protected by low hills to the northwest. On 25 November, with air temperature 48°, a clear sky, and a 15-mile northwest wind, both were visited but no butterflies were found, either flying or at rest. On 26 November, five male *C. eurytheme* were taken between 1040 and 1130 hours at Cheltenham with air temperature 50-52°F., clear sky, and wind 5 miles from the southwest. At Erdenheim five male and four female (one *alba*) were taken from 1300-1420 hours with temperature 58°, clear sky, and wind 10 miles from the southwest. More butterflies probably appeared at Cheltenham later in the day. One Erdenheim male was not fresh, but the other 13 butterflies were very fresh, and three were soft-winged.

In central New York, *C. eurytheme* was present continuously through 24 October. Heavy rain occurred on the 26th, followed by brief clearing the morning of the 27th and passage of a cold front in the afternoon. On the 27th two old *eurytheme* males were taken at rest in overcast (temperature 45°F.) at the Ithaca City Dump. A female *C. philodice* Latreille was also taken in flight during a sunny interval. Cloudy, windy weather then set

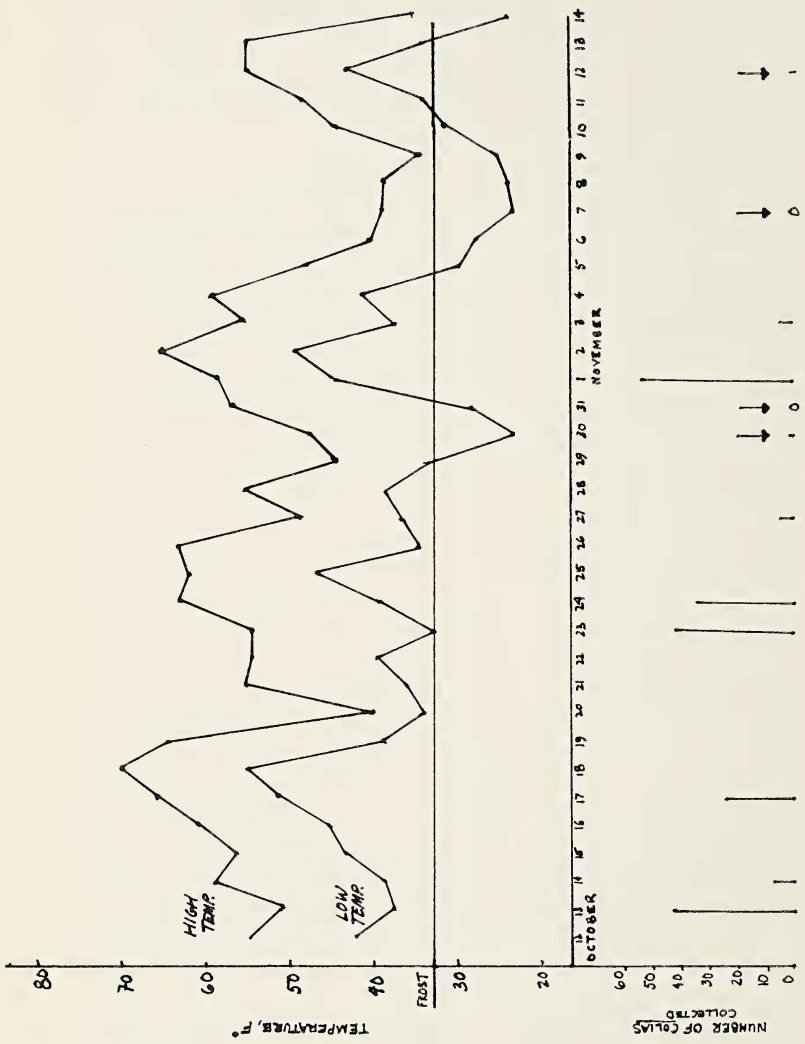

Fig. 3. Temperatures and *Colias* collections, October-November 1967. Ithaca, N.Y.

in. After a heavy freeze the morning of 30 October, a male *C. philodice* was taken on the Cornell University campus at 1400 hours with clear skies, a light southwesterly wind, and air temperature 46°F. A warm front passed on the 31st with heavy overcast. A "warm pocket" at Gracie, Cortland Co., was visited but no butterflies were found, despite an air temperature of 56°F. On 1 November it was clear, and *C. eurytheme* was found abundant at Gracie and at the City Dump. The air temperature in early afternoon was 58°. At Gracie 27 male and five female *eurytheme,* five male *philodice,* and five undetermined *alba* females were collected in 90 minutes; all but six were clearly fresh, and fourteen were newly eclosed and soft-winged. One male was taken sitting on its pupal case. The six older insects were obviously flown and might have emerged on the 30th or during the preceding warm period, before the 26th. There were only two freezes between the 26th and the 1st, but that of the 30th was quite severe. At the Dump eight male and two female *eurytheme,* including a pair in copula, and two male *philodice* were taken. All were very fresh.

The four *C. eurytheme* taken at the Dump on 3 November, and the one female taken there 12 November, were likewise all very fresh in appearance.

Reproduction and Selective Aspects. — Although reproduction by "false broods" would appear doomed, females of all three species usually contain a spermatophore when taken. Pairs in copula are common, and a great deal of sexual behavior, including male "darting-searching" of low vegetation and male-male chases, may be observed. This cannot be attributed to lack of flowers, as dandelions are usually present and visited repeatedly. As a behavioral adaptation to low temperatures, rapid initiation of sexual activity would be highly advantageous in insuring successful reproduction in the spring. A disproportion in sex ratio generally occurs in autumnal *Colias* emergences, with males two to four times as numerous as females. The same phenomenon occurs in the early stages of the spring emergence, but the sex ratio corrects itself in time. It is thus probably an artifact of the slightly slower development of the female. In both cases the result is generally the mating of unflown, newly-eclosed females, which may conserve energy for the latter. No differential sexual effect was noted in the arrestation experiments, except for a slight lag in the time of pigment deposition in the female pupae prior to arrest.

Mansingh and Smallman (1968) discuss precocious development in the Saturniid *Antheraea polyphemus* Cramer in North Dakota. This species is normally univoltine in the locality studied, and the timing of the single generation depends on weather conditions in the spring. An unusually early adult emergence from the overwintering pupae would permit some of their offspring to complete their development under non-diapause-inducing photoperiods and to emerge the same season (i.e. too late to reproduce), or to be frost-killed as pupae. These authors suggest that "early pupation can, under certain environmental conditions, become a serious mortality factor" in *A. polyphemus* (*loc. cit.*, p. 138). This is essentially analogous to the condition prevailing in the autumn broods of Pierids. Wastage of gametes at the end of the season should result in selective pressure for development of a timing mechanism effectively independent of temperature (i.e., photoperiodically induced diapause), except on a season-indicating threshold basis in mutlivoltine species. (*A. polyphemus* is partially or completely bivoltine southward, with a non-diapausing summer and a diapausing winter generation.) The duration of the developmental arrest should be adjusted to the onset of favorable conditions in the spring at each locality. This appears to be the case in *Pieris*. Both *P. rapae* and *P. protodice* are genetically polymorphic for duration of diapause under constant temperature conditions, and strains differing in induction ranges, temperature thresholds, and length of diapause can be selected (Shapiro, in preparation). Differences in microclimate undoubtedly maintain these polymorphisms in the population, resulting in a wide range of potential response to the year-to-year vagaries of weather.

In *Colias eurytheme* some sort of adjustment to winter survival appears to have taken place shortly after its invasion of the Northeast (Clark 1932). Although the species overwinters successfully every year at Philadelphia today, its tendency to produce a "false brood" is greater than that of any other Pierid species found there, and it still lacks a true diapause inducible in the larval stage. It begins to fly four to six weeks later than the *Pieris* species in spring, however, and the possibility exists that prolonged chilling may induce diapause or a diapause-like condition after pupation. Some half-grown larvae are apparently capable of overwintering at Philadelphia, but attempts to carry them through at Ithaca, outdoors or in a refrigerator, have failed.

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